Professor Ferguson

with the Author's Compliments.

REMARKS

ON THE

DENTITION OF BRITISH PULMONIFERA*.

BY

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[With a Plate.]

In venturing to offer a few remarks upon the Dentition of the Pulmonobranchiate Mollusca, I do so with much diffidence, partly on account of the paucity of species to be met with in the British Islands, and the absence of those connecting links without which no satisfactory conclusions can confidently be arrived at; but mainly from the conviction that those who first make observations upon a subject, which had previously been almost, or altogether, neglected, are much more liable to the commission of errors, alike in their microscopical examinations and in their physiological deductions, than those who have a foundation to work upon, be the works of their predecessors ever so erroneous. It is more, therefore, with the desire of calling attention

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to the subject, than with the intention of entering minutely into the form, structure and composition of these teeth, that I am induced to make some brief and general remarks upon them;—as foundation-stones, the friability or durability of which must be tested by future malacologists.

I am not aware of any papers having been published in England upon a detailed examination of the teeth of Mollusca, and but very few have appeared upon the continent. Prof. Lovèn of Stockholm has the credit of first proposing to employ this portion of their œconomy as a basis of classification, and his excellent paper on the subject may be found in the 'Proceedings of the Royal Swedish Academy*.' His observations are however chiefly upon the Marine Gasteropoda.

Herr Troschel has published some valuable remarks upon the dentition of some species amongst the Pulmonobranchiata; but (with the exception of some brief notices of the forms of a few unconnected species by different authors) I know of no other papers of importance in connection with this subject.

The tongue of the Pulmonobranchiata generally is a thin expansible membrane, two-thirds or three-fourths of which is rolled into a tube (Pl. IV. fig. 2 *c*); the posterior end of this tube is closed, while at its anterior extremity the remaining portion of the membrane is expanded into a flattened or spoon-shaped form, which plays against the edge of the horny upper jaw (fig. 2 *a*), thus acting more in the capacity of an under jaw than a true tongue. It is enclosed in the muscular head of the animal, and is connected with the œsophagus (fig. 2 *b*) at the anterior end of the tube, the extended upper portion of the œsophagus forming the roof of the mouth, while the expanded surface of the tongue covers the lower part of the mouth. The head is usually globular or nearly so, sometimes slightly attenuated backwards. From the junction of the tubes of the œsophagus and tongue, the former passes backwards through the head and leaves it at its upper part behind (sometimes coming out almost at the top of the head), while the tongue takes at once a downward and backward direction, and protrudes its closed end distinctly at the lower part of the head.

If the tubular part of the tongue be laid open and expanded (when it always proves of the same width as the naturally expanded portion), it will be found to be covered on its upper surface with a vast number of plates, each carrying one or more tubercles, which do not stand perpendicularly to the surface of the plates, but are abruptly curved posteriorly, so that the apices

* Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar, June 1847.

of these projections invariably point towards the closed end of the tongue (Pl. IV. figs. 3 & 4).

These teeth are distributed in rows all over the membrane, and are closely packed together. The longitudinal rows always consist of straight lines, but the transverse rows are variously curved, often bow-shaped, sometimes angular, rarely straight (figs. 12–19).

The degree of curvature of the transverse row, and the variations which the curves show (being sometimes composed of arcs of circles, while at other times they are made up of short straight lines lying in different directions), appear to depend on the form of the teeth. I shall allude to this again, after having described the teeth.

The number of teeth in a row does not seem to be always the same in individuals of the same species, though it may be pronounced as constant within certain limits. In different species, however, it is exceedingly variable: as a rule, there are more teeth in a longitudinal than in a transverse row, usually one-third or one-fourth more, though in *Helix Pomatia* the number in the transverse row exceeds that of the other, while in *Limnæus stagnalis* there are 110 in each direction.

Of the rows, taken longitudinally, I need not say much, it being more easy to explain the variations in the teeth, when the rows are regarded transversely. Suffice it to mention, that in the centre of the membrane there is a longitudinal row of teeth of different form to any of the rest.

It is to the form of the central tooth of the transverse row (the series of which constitutes the central longitudinal row just referred to) that I would wish to draw more particular attention; as I hope to show presently that all the other teeth partake more or less of the form of this tooth.

But before proceeding to its description, it will be well to explain the precise meaning of the terms I purpose using. From reference to an ideal vertical longitudinal section of a plate with its tubercle (Pl. IV. fig. 3), it will be evident that on viewing the whole vertically (Pl. IV. fig. 4) through the microscope (the object being almost transparent), three outlines will generally be seen, that of the *plate*, that of the attachment of the tubercle to the plate, which I shall refer to as the *base*, and that of the free point of the tubercle, which I shall speak of as the *apex*: the *tooth* will therefore be regarded as the plate and tubercle combined.

The central plate and its tubercle differ from all the others on the membrane in being symmetrical. The plate is of a subquadrangular form, often somewhat longer than broad, having its sides slightly hollowed out and its ends nearly straight

(*Limax*) (Pl. IV. fig. 5 *a*), or with its anterior end (that nearest the base of the tubercle) somewhat bow-shaped, in which cases this part overlaps the posterior straight edge of the plate in front of it (*Zonites radiatulus*) (fig. 1 *a*). In some it is nearly square (*Zonites*), while in others it presents the form of an inverted tapering triangle with a rounded apex (*Amphipeplea*).

The form of the tubercle on the central plate is subject to much greater variation than its plate. Sometimes the tubercle is very large and attached to nearly the whole surface of the plate, leaving but a small free apex (*Limax*) (Pl. IV. fig. 5 *a*) : in other species the tubercle is small and attached by its base to the anterior portion of the plate (*Zua*) (fig. 8 *a*). In another genus (*Planorbis*) we find that the tubercle is small and has two apices (fig. 9 *a*). The apex in some few instances projects beyond the edge of the plate, and consequently lies above the base of the tooth next behind it ; but in the majority of cases, the apex of the *central* tubercle does not project over the edge of its plate.

The lateral plates not only differ from the central one in form, but also from each other as they approach the edge of the membrane. The general form is subquadrilateral, the anterior and posterior edges being subject to the same variations as those described with reference to the central plate, while the inner edge is always more or less convex and the outer edge concave. In those species where the curve of the horizontal row is considerable, the plates as they approach the edge get narrower, and in these it is not unusual for them also to assume somewhat an S-form on the one side and its reverse on the other. In others, however, the lateral plates become gradually broader, and eventually twice as broad as the primary lateral plates.

I come now to speak of the lateral tubercles ; but as they vary nearly as much in the same individual as they do in different species, it would be an almost endless task to describe all the forms they assume. A careful examination of them generally shows, I think, clearly, that the following rule may be laid down regarding their form.

If an ideal line be drawn longitudinally through the central tubercle, so as to divide it equally, it will be found that the two halves are precisely similar (Pl. IV. fig. 4) ; but such is not the case with any of the lateral tubercles. We find, too, that those lateral tubercles which are nearest to the central tubercle are always more similar to it in general form than those at the edge ; indeed, that the tubercles become more unlike the central tubercle as their position is nearer to the edge of the membrane. Hence I deduce the following rule : viz. that the lateral tubercles are merely modifications of the form of the central tubercle ; and

that these modifications are effected by the *suppression* of the prominences on the *inner* side of each lateral tubercle, and the simultaneous *increase* of the corresponding parts on the *outer* side. By the "inner" and "outer" sides, I mean the side nearest to, or farthest from, the central tooth.

In *Limax carinatus* and some allied species we have this rule clearly exemplified, the change from the typical form into that at the edge being very gradual, and showing every possible connecting link (Pl. IV. figs. 5, 6, 7). But this gradual progression is far from being the case in all species: the sudden and abrupt change in form which is seen in the fourth lateral tubercle of *Zonites radiatulus* (fig. 1 *c*) might at first sight seem to overthrow this rule; but on comparing this tongue with others, where the central tooth is somewhat similar and the modification of the lateral tubercles more gradual, it will be at once perceived that this sudden change of form is owing to the *absence* of the connecting links, which a reference to the progressive alteration in other species will readily supply, if not actually, at any rate to the imagination; and it will be found that an application of the rule I have laid down, to the third lateral of *Zonites radiatulus*, would eventually bring out the form of the fourth lateral, though the connection would, I grant, require several plates to complete it. I would now be permitted again to refer to the directions assumed by the horizontal rows, which (as I previously mentioned) depend upon the form of the teeth. Wherever a straight line is observable in the arrangement of the lateral teeth, it will be found that all the teeth in that line are similarly formed, whether the right and left laterals are in the same line as in *Planorbis contortus* (fig. 12), or divaricate from each other at the central tooth, upwards as in *Achatina acicula* (fig. 15), or downwards as in *Ancylus fluviatilis* (fig. 13). Wherever the curve presents great angularity (as in *Zonites radiatulus*) (fig. 14), there we find a sudden change in the form of the teeth, while in like manner a gradual curve is the result of a gradually progressive change in the form of the teeth, the degree of deviation from a straight line being exactly in proportion to the amount of change which takes place between the form of the central and edge-teeth.

It may perhaps seem that I have dwelt at greater length on this point than was necessary; but as there are many species of Pulmonobranchiata so small as to render it difficult with the best glasses to determine the form of the plate and often of the tubercle, the attachment of the tubercle to the plate being the only part clearly visible, it appears to me desirable that the following rules should be laid down with reference to the form of the lateral teeth, in connection with the horizontal rows.

A *straight line* indicates similarity in the teeth; a *curve* indicates a GRADUAL change in their form, and an *angularity* in the row indicates a SUDDEN change.

Having stated in general terms what are the usual characteristics of the teeth amongst the Pulmonobranchiata, I purpose now to offer a few observations upon those variations in them which seem to be characteristic of certain genera and families; prefacing these remarks with a list of the species I have had an opportunity of examining.

Arion ater.
Limax maximus.
—— carinatus.
Vitrina pellucida.
Helix aspersa.
—— hortensis.
—— nemoralis.
—— Pomatia.
—— arbustorum.
—— obvoluta.
—— lapicida.
—— pulchella.
—— Cantiana.
—— Carthusiana.
—— fulva.
—— concinna.
—— Pisana.
—— virgata.
—— caperata.
—— ericetorum.
Zonites rotundatus.
—— alliarius.
—— cellarius.
—— nitidulus.
—— radiatulus.
Succinea putris.
Bulimus Lackamensis.
Bulimus obscurus.
—— acutus.
Zua lubrica.
Achatina acicula.
Pupa marginata.
—— juniperi.
Vertigo edentula.
—— pygmæa.
Balæa perversa.
Clausilia bidens.
—— nigricans.
Carychium minimum.
Limnæus pereger.
—— stagnalis.
—— palustris.
Amphipeplea glutinosa.
Ancylus fluviatilis.
Velletia lacustris.
Physa fontinalis.
Planorbis corneus.
—— albus.
—— carinatus.
—— marginatus.
—— nitidus.
—— contortus.
Segmentina lineata.
Cyclostoma elegans.

Since this list comprises little more than half our British species, it would be hazardous to attempt to deduce any positive theories as to the constancy of form in any particular groups. Indeed, it would not be safe to lay down any rules even from an examination of all the British species, since many in the same genus present such marked differences, alike in external form and in the conformation of their teeth, that it would be impossible to arrive at any satisfactory deductions, without the opportunity of examining the connecting links which foreign species will supply.

In the list I have given, the names and arrangement are those used in the last edition of Turton's 'Manual,' and on the whole, the form of the teeth is confirmatory of this classification. The *Arionidæ* and *Limacidæ* are much alike, and differ from the

Helicidæ in having a long projecting single apex to the edge-teeth. The *Helicidæ*, on the other hand, show a marked disposition to increase the number of apices by bifurcation as they approach the edge.

Arion ater. Limax maximus. —— carinatus. Vitrina pellucida. Zonites alliarius. —— cellarius. —— nitidulus. —— radiatulus.	Edge-teeth aculeate.
Helix fulva. —— aspersa. —— Pomatia. Zonites rotundatus. &c. &c.	Edge-teeth serrate.

Vitrina evidently belongs more to the *Limacidæ* than the *Helicidæ*, as is shown by the single prolonged apex to the edge-teeth. From the very similar character of the edge-teeth in *Zonites alliarius, cellarius, nitidulus* and *radiatulus* (whose tongues *greatly* resemble each other), I am induced to believe that they should come in between *Vitrina* and the true *Helices*, for while their edge-teeth show no appearance of bifurcation, the heel to the apex may possibly be looked upon as an approach towards it. Their sagittate central tubercle corresponds with that of *Vitrina*, and a similarly-shaped central tubercle in *Helix fulva* connects them with the true *Helices*, which have a simple aculeate tubercle. *Zonites radiatus* (or *rotundatus*) is a true *Helix*.

Succinea putris, from its partiality for the leaves of plants growing in the water and for other very wet places, might possibly be expected to show some change towards the form of a *Limnæus* in its teeth, whereas on the contrary they are truly Helicine in their conformation. So also are the teeth of all the other *Helicidæ* that I have examined, though they of course present specific characters more or less conspicuous. I imagine however that it will be more difficult to fix upon good generic characters in the teeth of the *Helicidæ*, than any other family. *Zua* and *Achatina* should perhaps come at the end of the list, as their very small central tubercle corresponds with that in the genus *Limnæus*. The genera *Pupa* and *Vertigo* present no apparent difference, and have their central tubercle much of the same form as *Zua* and *Achatina*, but in these it is as large as the primary lateral tubercles.

The character of *Limnæus* appears to be, to have one small central tubercle, as it were "squeezed up" between two very large lateral ones, each primary lateral having a very large apex

internally with a small external one, while at the edge they have altered to one thick prolonged apex projecting inwards and irregularly lobed on its upper edge. Much the same arrangement prevails in *Amphipeplea*, where however the tubercle of the lateral teeth is even still larger, in proportion to its plate.

Ancylus and *Velletia* present widely distinct characters, clearly showing that they do not belong to one genus. In *Ancylus* there are thirty similar lateral teeth in a straight line on each side of the central tooth, and then there is a slight curve through a series of six more teeth where a trifling change in their form occurs. In *Velletia*, on the contrary, no part of the horizontal row is straight; its central part is much arched, and is composed of the central tooth and twelve lateral teeth on each side which do not alter much in form. Then comes one tooth of a different form, and lastly six more on each side, which latter are in a slight curve.

Physa, again, exhibits a multitude of teeth of a similar form, though different to any that I have seen in other genera; but unfortunately, owing to the delicacy of the tongue-membrane, I have failed in ascertaining either the form of the central tooth, or the curve of the horizontal row.

Planorbis appears to be governed (as botanists would say) by the number three. Its primary lateral tubercles have three apices, and the central tubercle, generally in the genus, has two apices placed far apart from each other (Pl. IV. fig. 9 *a*) : this appears to be merely the result of the suppression of the third intermediate apex, a view in which I am borne out by a specimen of *P. marginatus*, in which there is only one side apex to the central tooth, the central apex and that on the other side being both suppressed.

Of *Segmentina* and a few others I will not now speak, having failed in meeting with glasses good enough to bring out their forms clearly. The last species on my list is *Cyclostoma*; but as this belongs to a section of the Pulmonobranchiata differing so widely from that to which the subjects of my preceding remarks belong, I will not describe it, but merely call attention to the general aspect of its tongue, which much resembles that of some of the fluviatile Pectinibranchiates; to these species the *Cyclostoma* presents some analogy, in being unisexual, and operculated, in having but two tentacles, with its eyes placed at their base on their outer sides, and in being a vegetable feeder.

It will be desirable, perhaps, before I conclude this paper, that I should give some idea of the number of teeth in a transverse or horizontal row in a few species, together with the number of those rows upon the tongue, and the whole number of teeth on that organ. And to this I propose to add also, the actual

size of the individual teeth of one or two species, to show their minuteness.

	Number of transverse rows.	Number of teeth in row.	Number of teeth on tongue.
Arion ater	160	110	17,600
Limax maximus	160	180	26,800
—— carinatus	80	100	8,000
Vitrina pellucida	100	75	7,500
Helix aspersa	135	105	14,175
—— nemoralis	135	100	13,500
—— Pomatia	140	150	21,000
—— obvoluta	170	90	15,300
—— lapicida	150	80	12,000
—— pulchella	65	30	1,950
—— Cantiana	125	80	10,000
—— fulva	70	45	3,150
—— concinna	100	50	5,000
—— Pisana	120	70	8,400
—— caperata	100	45	4,500
—— ericetorum	115	60	6,900
Zonites alliarius	45	25	1,125
—— cellarius	35	27	945
—— nitidulus	55	65	3,575
Succinea putris	50	65	3,250
Bulimus obscurus	120	55	6,600
—— acutus	100	37	3,700
Zua lubrica	80	40	3,200
Pupa juniperi	100	40	4,000
Balæa perversa	130	40	5,200
Clausilia bidens	120	50	6,000
—— nigricans	90	40	3,600
Limnæus stagnalis	110	110	12,100
Ancylus fluviatilis	120	75	9,000
Velletia lacustris	75	40	3,000

It will I think be readily conceded, from a glance at this table, that the number of teeth upon a tongue is never likely to be of more than *specific* value as a characteristic feature, since there appears to be no general number, or even approximate number, which can be said to belong to any genus. Since *Limax maximus* heads the list with 27,000, and *Helix Pomatia* follows with 21,000, it might be conjectured, perhaps, that *size* had some influence in the matter; but then we find *Helix aspersa* and *nemoralis* possessing nearly the same number, while *Helix obvoluta*, a shell very little, if at all, larger than *Zonites cellarius*, possesses more than *fifteen* times the number of teeth.

With reference to the actual size of some of the teeth, it will be most convenient to take the 10,000th of an inch as the measuring standard; and therefore the numbers that I shall

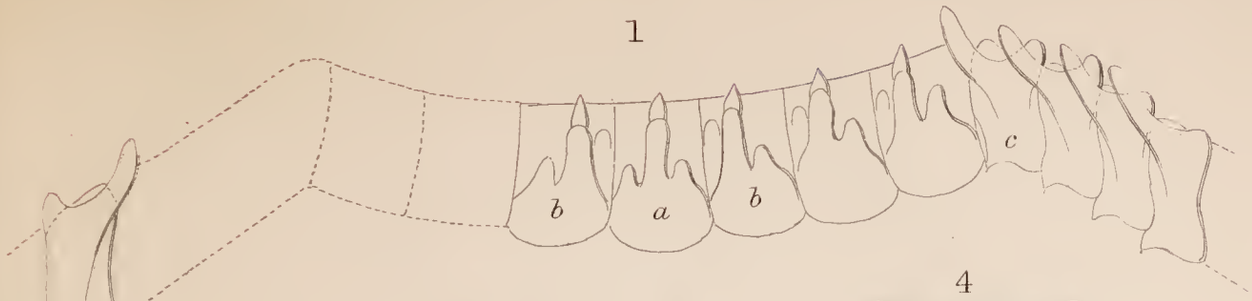
now use, in giving the dimensions of the teeth, are to be regarded as so many 10,000ths of an inch.

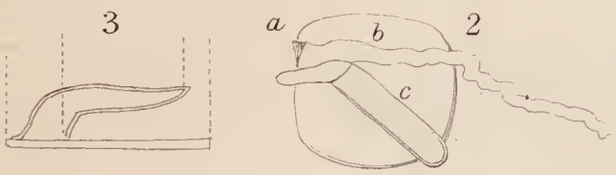
In *Arion ater*, the central and neighbouring plates are 25 long by 15 wide. In *Limax maximus* they are 20 long and $11\frac{1}{2}$ wide. In *Bulimus obscurus* the length of the plates is 7, while the average breadth of all in the row is $4\frac{2}{5}$. In *Zua lubrica* the length is $5\frac{1}{2}$ and the average breadth $4\frac{1}{2}$. In *Clausilia nigricans* the length is $4\frac{1}{2}$ and the average breadth $3\frac{2}{3}$. The primary lateral plates of *Limnæus stagnalis* are 22 long by $14\frac{2}{3}$ wide. In *Amphipeplea glutinosa*, the corresponding plates are $11\frac{1}{2}$ long and 10 wide, which happens to be precisely the size of the primary lateral plates in *Planorbis corneus*.

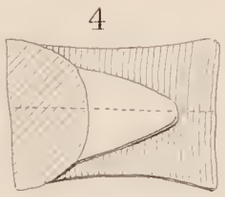
King's College, July 1850.

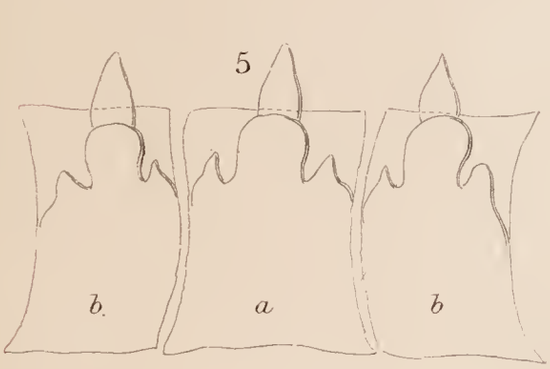
EXPLANATION OF PLATE IV.

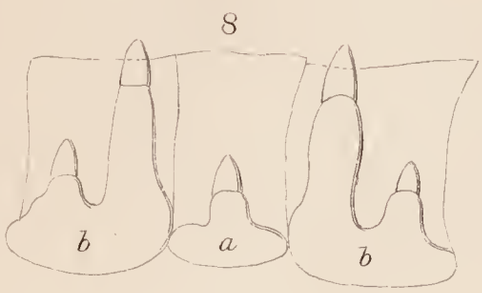
Fig. 1. Central portion of transverse row of *Zonites radiatulus*: *a*, central tooth; *b*, first lateral; *c*, fourth lateral tooth.
— 2. Head of a Snail: *a*, horny tooth; *b*, œsophagus; *c*, tongue.
— 3. Diagram of a vertical section of a tooth.
— 4. Ditto central tooth.
— 5. *Limax carinatus*: *a*, central tooth; *b*, first lateral.
— 6. Ditto an intermediate lateral tooth.
— 7. Ditto edge-tooth.
— 8. *Zua lubrica* (*a*, *b*, as above).
— 9. *Planorbis carinatus* (*a*, *b*, as above).
— 10. Ditto an intermediate lateral tooth.
— 11. Ditto edge-tooth.
— 12–19. Direction of transverse rows:—
— 12. *Planorbis contortus*.
— 13. *Ancylus fluviatilis*.
— 14. *Zonites radiatulus*.
— 15. *Achatina acicula*.
Fig. 16. *Zua lubrica*.
— 17. *Vitrina pellucida*.
— 18. *Limax carinatus*.
— 19. *Helix obvoluta*.

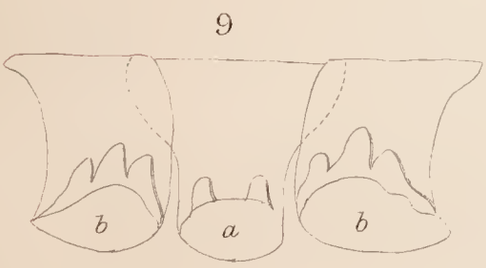


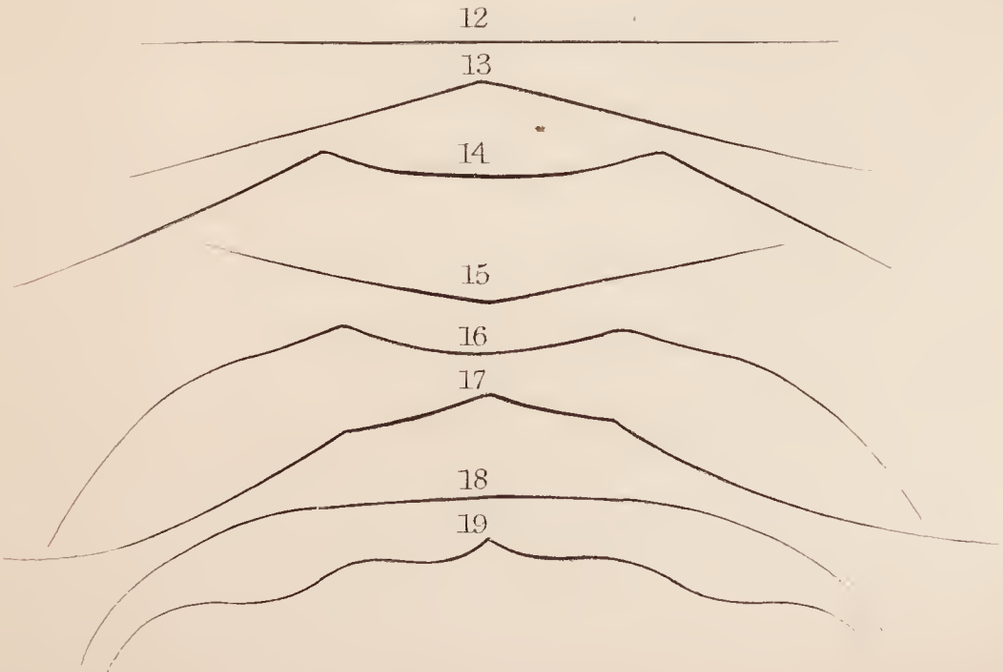












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